

Further Studies on Factors Influencing the Reactions of Tropical Shore Fishes to Shells

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(Plates I & II)

INTRODUCTION

IN a study of the reactions of fishes which normally seek shelter in shells, it was found that the whole problem could be somewhat simplified by substituting simple tetrahedrons with a single opening, Breder (1950). The present contribution is an extension of that study. In the earlier work cardboard and concrete tetrahedrons were used. It was found that the two species employed, young *Pomacentrus leucostictus* Müller & Troschel and mature *Bathygobius soporator* (Cuvier & Valenciennes), accepted the concrete boxes as readily as shells, but that they would not spend the night in the cardboard boxes, although these were of identical form. It was thought that the slight flexibility of the water-soaked cardboard made these boxes an insufficiently rigid substitute for the stone-hard shells customarily used by these fishes. For purposes of the new series of experiments the same concrete tetrahedrons were used and in addition one which was made of glass. A black cardboard cover was made that would fit snugly over the glass construction. The aquariums used were the same as in the earlier series of experiments, 2' × 1' × 1'. They were supplied with running sea water. Like the others, these experiments were carried out at the Lerner Marine Laboratory on Bimini, Bahamas. They occupied a period between November 24 and December 10, 1953. These dates are mentioned mainly because fighting is at a minimum among such fishes at this season, with its cooler water, whereas in the warmer seasons fighting may be pursued with vigor, sometimes to the destruction of some of the participants.

The constructional details of the concrete tetrahedrons have been given by Breder (1950). Those of the glass tetrahedron, which was made

as much like the concrete constructions as possible, follow. Four identical equilateral triangles were cut from a piece of double-thick window-glass with an ordinary steel-wheel glass cutter. Each triangle was given an altitude of 4 inches. A "doorway" was provided in one of them by the following procedure. First it was cut into three pieces by two cuts, parallel and to either side of an altitude. The central strip so obtained was then cut into three pieces by two cuts parallel to the base of the triangle. The middle piece, representing the "door," was removed and the remaining four pieces reassembled and cemented together with transparent Duco cement, leaving a rectangular "doorway" similar to those in the concrete shelters. The details of this may be best seen in Plate I, Figure 2, and Plate II, Figure 5. After the reassembled triangle with the "doorway" had become firm enough to handle, the four triangles were then cemented together to form a tetrahedron, all with transparent Duco cement. The bottom triangle together with the basal edges of the other three were then set in a thin layer of concrete in order to insure complete rigidity. This base cannot be seen in the photographs, as it is buried in the sand to a depth similar to the bases of the concrete tetrahedrons. Thus the floors of both the glass and the concrete shelters presented an identical condition: concrete, covered with a thin layer of sand.

Critical reading of the manuscript by Dr. T. C. Schneirla is gratefully acknowledged.

EXPERIMENTS

Young *Pomacentrus* were handled in the following manner. Three fish were established in an aquarium with three similar concrete tetrahedrons. As is usual with this species, each individual appropriated one of the shelters as its

own. Two days later the glass tetrahedron was added to the aquarium. Except for the general attention these fish give to any small new object introduced into their aquarium, no special response was given to it and no evidence was seen of any apparent perception of it as a possible place to enter. This condition continued for three days, when the experiment was terminated.

Two new *Pomacentrus* were established in an aquarium with one concrete tetrahedron and the glass one. They behaved similarly to the fish in the previous experiment, the concrete "house" being quickly taken and the glass one not entered. The odd fish merely hid in a corner and when disturbed swam from one corner to another. At another time, when both fish were foraging, a slight disturbance caused them to beat a hasty retreat, both to the concrete chamber. In so doing one of the fish bumped into the glass shelter, evidently attempting to swim through it as fish will sometimes do on encountering the glass side of an aquarium. Certainly there was no recognition of it as a place of retreat.

The following day a black cardboard cover was placed over the glass tetrahedron. It was then occupied within five minutes. This situation is shown in Plate I, Figure 1. On removal of the cover the fish promptly swam into the concrete shelter. When the cover was replaced the fish returned. This performance could be repeated at will. It is to be noted that the other fish continually occupied the concrete shelter and that two of these young fish will not occupy one shell for long—and then only when there is considerable provocation.

The behavior of *Bathygobius* when confronted with the same situation is strikingly similar but with a few interesting modifications. In the first experiment with these fish, two were placed in an aquarium with only the glass tetrahedron present. Both the fish hid in corners and gave no attention whatsoever to the glass shelter. A concrete shelter was added the next day and it was immediately occupied by the evidently dominant fish, the other continuing to occupy a corner. Plate I, Figure 2, shows this condition with the shelterless fish foraging. This situation continued for four days at the end of which time sand was piled about the glass chamber to about half way up its sides. After this had been done the odd fish would enter it but only under conditions of vigorous disturbance, *i.e.* by being chased about by means of a glass rod. The results of this are shown in Plate I, Figure 3.

Two new fish were established in an identical arrangement and their behavior was like that of the previous two. On the second day the

glass chamber was covered with black cardboard, after which it was promptly occupied, as is shown in Plate II, Figure 4. When the cover was removed, four days later, the fish showed behavior which had not been anticipated. Instead of merely swimming out of the construction, as had the *Pomacentrus* under identical conditions, the *Bathygobius* showed what appeared to be a state of "confusion." The fish was seen, on removal of the cover, to be adhering upside down near the apex of the tetrahedron, a position not unusual with these fishes. It continued to cling with its pelvic suction disc for a moment and then descended to the floor of the chamber where it executed a series of attempts to force its way through the now transparent walls. It worked back and forth along the two walls without an opening, in evident confusion, before finding the doorway which it formerly had been using regularly and with certainty. Once emerged from the glass shelter, it immediately and with no hesitancy entered the concrete retreat. On replacement of the cover the fish reentered the glass "house" within five minutes.

An hour later the cover was once again removed, whereupon the fish dropped to the floor and quietly and promptly left through the doorway, with no evidence of confusion, after which it entered the concrete shelter as before. A similar trial three hours later again revealed some of the earlier confusion, but not nearly so marked. The two fish were then left undisturbed for four days. At the end of this time removal of the cover produced confusion equal to that seen the first time it was tried. As in the first trial, the fish seemed to insist on finding an exit every place except through the doorway. This experiment could be repeated at will, the amount of "confusion" induced being very nearly directly proportional to the length of time the black cover had remained in place. Plate II, Figure 5, shows conditions as the cover was being removed. The cover is still partly in the water, in the upper left, and the fish is in its typical position, just a moment before it dropped to the floor of the chamber.

DISCUSSION

As noted by Longley & Hildebrand (1941) and Breder (1950), *Pomacentrus* is strictly diurnal and spends the dark hours entirely within the shelter of its selection. While individuals may have some slight contact with the cavity they inhabit, such as with the tips of the pectoral or pelvic fins, they are not ordinarily in intimate contact with the walls or floor of their shelter. *Bathygobius*, on the other hand, is practically aperiodic in habit and does have con-

tinual intimate contact with the walls or floor of the shelter, always resting on the bottom or hanging on the walls or ceiling by means of its pelvic suction disc. For this reason it was thought that there might be some marked difference between the reactions of *Bathygobius* to a transparent shelter and those of *Pomacentrus*, on the assumption that much of the behavior in reference to shelters shown by the former is dependent on tactile cues, whereas that of the latter would seem to be largely, if not entirely, visual.

Before going into a discussion of the experimental results it is necessary to point out that in the earlier work on these species in aquaria there was noted a reluctance on the part of well-established fishes to enter a newly introduced shelter, although it would be thoroughly "inspected." It is to be especially noted that in the present experiments, in each case where the glass shelter was introduced the fish could not, in any sense, be considered as well established. They were merely given sufficient time to get well over their initial fright incident to netting and general handling before the experiments were started. These various details of behavior, together with the other items noted, especially as shown by the experiments with the black cover, indicated clearly that it is the transparency of the glass shelter which prevents its normal use by both species. The tactile cues which *Bathygobius* receives over and above the chiefly non-tactile cues received by *Pomacentrus*, are evidently insufficient to make any marked difference in the attitudes of the two species toward transparent shelters.

It is to be noted that in the earlier study it was possible to write as follows regarding the introduction of opaque objects into the aquaria: "As is obvious from the most casual observations, these experiments confirm the fact that both species under discussion are acutely aware of the physical features of their environment. They both spend much time swimming around and nosing into crevices of any new object or one which has been turned around or otherwise disturbed. As was noted by Breder (1949), they also will frequently return an object to its original site if they are capable of doing it. *Bathygobius* generally perches itself on the new object after it has 'inspected' it for a time, perhaps obtaining further sensory data through the pelvic sucker. *Pomacentrus*, on the other hand, seldom touches such objects." In none of the present experiments was the glass retreat "inspected" or touched in any exploratory sense by either species. This is the more remarkable for, as can be seen in the photographs, the glass was not perfectly clear, be-

cause of the settling of detritus, although at all times distinct vision through the glass was possible.

The confusion effect noted in the case of *Bathygobius*, but not in *Pomacentrus*, may indeed be a measure of the difference between these two fishes in respect to the differing nature of their manner of obtaining sensory cues. In the latter, clearly dominated by visual cues, there was no confusion whatever and an opening remained "a doorway" even if the surrounding walls suddenly became transparent. *Bathygobius*, on the other hand, always in contact with some solid except when actively swimming, showed confused responses. Swimming, in this species, is never long nor continuous, but is more in the nature of short hops from place to place. It is nevertheless difficult to account for the failure of these fish to recognize the normally-used doorway. Beebe (1931) noted that individuals removed from a tidepool to another usually returned to their original home pool without difficulty. Aronson (1951) in other connections concerning the tidepools which these fishes often inhabit, found them to have a normal, if not superior, fish-memory for places and the location of objects, exits and the like. The work of Goldsmith (1905, 1912, 1914) on the topographic memory of *Gobius minutus* Linnaeus gives similar data on a related species. Thus the evidence from both the present and earlier studies (Breder 1948, 1949, 1950) and from the above references reinforces the idea that these fishes have a very acute "awareness" of the micro-geographic details of their immediate environment and a considerable retention as to the nature of those details.

It is consequently believed that the confusion of gobies in glass retreats suddenly uncovered is not rooted in any inadequacy of either memory or awareness of objects and their locations. It is thought, rather, that this failure to escape promptly from a retreat which has suddenly become transparent is rooted in a breakdown of whatever integrative mechanism is involved. The failure to react appropriately to a transparent wall of glass suggests a characteristic inability to recognize a transparent solid for what it is. Ordinarily in the environment in which these fishes live, the ability to see the view ahead also means the ability to move ahead. It should be recalled that some fishes never learn to respect the glass walls of an ordinary aquarium while others do so in a very short time. Also, it may be noted, well-established gobies will often adhere to the transparent glass sides of their aquarium while newly introduced ones will do this only where the corner angles present the surface as an opaque solid. At such

times newly introduced fish will still try to swim through the sides. Eventually they seem to become accustomed to the glass walls but seemingly never to the point where a piece of food offered from the outside or a fly alighting on the glass wall will fail to elicit a feeding response.

Although bottles of various kinds are present in the sea-bottom environment of these fishes and are not infrequently occupied by either species, they are, for the most part, covered with marine growths, half buried in sand or made of brown or green glass. Experiments made with clear glass bottles in the sea indicate that while not many gobies will enter the mouths of small-mouthed bottles, when they do they have difficulties in finding their way out. This behavior, on a basis of appearance, would seem to be identical with that found in connection with the glass tetrahedron. The infrequency of entry into such bottles by either species is apparently associated with some difficulty in finding such a small opening in a transparent object.

When the opening is made more accessible we have, in effect, a fish trap. In their more common forms the glass or plastic minnow traps take advantage of this situation, as indeed do wire traps or fykes or other devices where the fish can see ahead but are not able to swim ahead. Of course, in addition, these traps are usually baited and the mouth is made easy to find from the outside but hard to find from the inside by some expression of the simple funnel principle. In the case of a common bottle the "funnel" actually points the wrong way, from a fish trapper's point of view. That a simple clear bottle or a glass tetrahedron (with which the fish was habituated) should so confuse such a fish is somewhat surprising.

All this suggests that visual stimuli and tactile stimuli are closely integrated in the case of *Bathygobius*. If this can be accepted, then the reversal of one (transparency where opaqueness would be expected) with no modification of the associated tactile stimuli might well lead to inadequate responses on the part of the fish. The two sets of stimuli are then no longer acting in the normal unison with which the individual has had experience. *Pomacentrus* has no such problem, because of the minor or absent role of contact in the totality of its responses to solids.

These experiments would seem to indicate that any thigmotropic effect operating in the case of *Bathygobius* is insufficient to override the visual cues to a point where the fish can

accept a transparent shelter. Further than this, if an opaque shelter has been accepted by a fish and then is suddenly rendered transparent, whatever positive thigmotaxis may be involved is clearly insufficient to prevent immediate rejection of the shelter.

Bathygobius shows a wide variety of changeable color patterns which have been described in general terms by Beebe (1931), discussed as to some of their significance by Breder (1943, 1949) and described in much greater detail by Tavolga (1950) who included a demonstration that different populations showed differences in the range of patterns displayed. Because of these differences and the behavior herein discussed, it would appear that this species should present favorable material for a more refined study. The interaction between the acceptance of differing kinds of retreats by individuals differing in physiological and psychological condition, as indicated by the pattern shown, should be amenable to experimental approach. A comparative study of how these two kinds of behavior, pattern change and shelter entry, are modified in populations differing as to the range and scope of patterns regularly displayed, should be illuminating.

SUMMARY

1. Young *Pomacentrus leucostictus* and mature *Bathygobius soporator* will accept small artificial concrete shelters for occupancy in aquaria.
2. The same individuals will completely disregard clear glass shelters of the same design.
3. They will accept the glass ones if they are made opaque by covering with a black paper cap.
4. Removal of such an opaque cap will cause the *Pomacentrus* to leave directly and rapidly.
5. Removal of such an opaque cap will cause *Bathygobius* to enter a state of "confusion" wherein it attempts to leave through the glass walls at practically every point except the doorway which it had been using previously, before it finally finds its way out.
6. This confusion lessens with repeated trials but returns again in force if a few days elapse between trials.
7. The confusion is evidently not rooted in either faulty memory or inadequate knowledge of the details of the immediate environment, but rather in an inability to "comprehend" the nature of a transparent solid.

8. The difference between *Pomacentrus* and *Bathygobius* in this respect is evidently based on the fact that the former receives chiefly visual cues from solids whereas the latter receives both visual and tactile cues from such objects, the failure of the two types of stimuli to properly integrate producing the observed confusion.

REFERENCES

ARONSON, L. R.

1951. Orientation and jumping behavior in the gobiid fish *Bathygobius soporator*. Amer. Mus. Novitates, (1486): 1-22.

BEEBE, W.

1931. Notes on the gill-finned goby, *Bathygobius soporator* (Cuvier and Valenciennes). Zoologica, 12 (5): 55-66.

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1943. The eggs of *Bathygobius soporator* (Cuvier and Valenciennes) with a discussion of other non-spherical teleost eggs. Bull. Bingham Oceanogr. Coll., 8 (3): 1-49.
1948. Observations on coloration in reference to behavior in tidepool and other ma-

rine shore fishes. Bull. Amer. Mus. Nat. Hist., 92 (5): 281-312.

1949. On the relationship of social behavior to pigmentation in tropical shore fishes. *Ibid.*, 94 (2): 83-106.

1950. Factors influencing the establishment of residence in shells by tropical shore fishes. Zoologica, 35 (12): 153-158.

GOLDSMITH, M.

1905. Recherches sur la psychologie de quelques poissons littoraux. Bull. Inst. Gén. Psychol., 5: 51-67.

1912. Contribution à l'étude de la mémoire chez les poissons. *Ibid.*, 12: 161-176.

1914. Les réactions physiologiques et psychiques des poissons. *Ibid.*, 14: 97-228.

LONGLEY, W. H. & S. F. HILDEBRAND

1941. Systematic catalogue of the fishes of Tortugas, Florida with observations on color, habits, and local distribution. Papers Tortugas Lab., 34, Carnegie Inst. Washington Publ. (535): 1-331.

TAVOLGA, W. N.

1950. Pattern variability among populations of the gobiid fish *Bathygobius soporator*. Copeia, (3): 182-194.

EXPLANATION OF THE PLATES

PLATE I

Behavior of fishes in reference to standardized retreats.

- FIG. 1. Two *Pomacentrus* occupying respectively a concrete and a covered transparent shelter.
- FIG. 2. Two *Bathygobius*, one occupying a concrete shelter and the other refusing a transparent shelter.
- FIG. 3. The two fish of Fig. 2 after sand has been banked about the transparent shelter.

PLATE II

Behavior of fishes in reference to standardized retreats.

- FIG. 4. The two fish of Plate I, Figs. 2 and 3, after the transparent shelter has been covered.
- FIG. 5. Detail of the position generally taken by the occupant of the glass shelter. This photograph was taken the moment the cover was removed and before the fish had dropped to the floor of the chamber. The cover may be seen in the upper left corner and the near corner of the concrete chamber in the lower right. Photographs by Carol Mosher.